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Cleaning in pairs enhances honesty in male cleaning gobies

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A recent game theoretic model akin to an iterated prisoner's dilemma explored situations in which 2 individuals (the service providers) interact simultaneously with the same service recipient (the client). If providing a dishonest service pays, then each service provider may be tempted to cheat before its partner, even if cheating causes the client's departure; however, a theoretical cooperative solution also exists where both partners should reduce cheating rates. This prediction is supported by indirect measures of cheating (i.e., inferred from client responses) by pairs of Indo-Pacific bluestreak cleaner wrasses *Labroides dimidiatus*. Here, we examine how inspecting in pairs affects service quality in Caribbean cleaning gobies *Elacatinus* spp. We measured dishonesty directly by examining the stomach contents of solitary and paired individuals and calculating the ratio of scales to ectoparasites ingested. We found that the propensity to cheat of females and males differed: females always cleaned relatively honestly, whereas males cheated less when cleaning in pairs than when cleaning alone. However, overall, the cleaning service of single and paired individuals was similar. Our results confirm that cleaners cooperate when cleaning in pairs; however, our findings differ from the specific predictions of the model and the observations on *L. dimidiatus*. The differences may be due to differences in mating systems and cleaner–client interactions between the 2 cleaner fish species. *Key words:* cooperation, *Elacatinus* spp., honesty, iterated prisoners', dilemma, singles versus pairs. *[Behav Ecol 20:1343–1347 (2009)]*

The iterated prisoner's dilemma (IPD) game illustrates why stable cooperation between unrelated individuals may be difficult to achieve: although 2 partners receive a higher payoff from mutual cooperation than they do from mutual defection, cheating is more beneficial than cooperating in each encounter, regardless of partner behavior (Axelrod and Hamilton 1981). This dilemma may explain why cooperative solutions to the IPD seem to be rare in nature (Hammerstein 2003).

Recently, however, Bshary et al. (2008) developed and tested a new game theoretic model that is akin to an IPD under a wide parameter space. They explored a situation where one class of players provides a service to a second class of players (the clients). They assumed that 1) the benefits of the service yield diminishing returns to the service provider, 2) service providers may gain additional benefits from cheating, and 3) cheating may lead to the immediate departure of the client. The analytical model yielded 2 evolutionarily stable strategies to adopt when 2 service providers interact simultaneously with the same client. The noncooperative solution predicts that each of the 2 service providers should try to cheat immediately, yielding a complete breakdown of service quality. In contrast, the cooperative solution in an iterated game predicts that service quality in pairs should be higher than that provided by singletons; otherwise, pair inspections would last just half as long as singleton inspections, which would be a suboptimal solution to the trade-off between accepting diminishing returns and cheating but spending more time without any client.

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Marine cleaning mutualisms provide an ideal system to test how service quality is influenced by the number of service providers. Cleaner fish cooperate with their fish clients by removing ectoparasites and cheat by eating mucus and scales (Arnal and Côté 2000; Cheney and Côté 2001, 2003, 2005; Bshary and Grutter 2002; Whiteman and Côté 2002a, 2002b; Grutter and Bshary 2003; Grutter and Bshary 2004; Sikkel et al. 2004; Soares, Bshary, Cardoso, and Côté 2008a). Nonparasitic items may, in some cases, be the preferred food (Grutter and Bshary 2003). In addition, cleaners may inspect clients alone or in pairs composed of a male and a female (Whiteman and Côté 2002a, 2002b, 2003; Bshary et al. 2008). During pair inspections, the benefits of cheating can be gained by only one cleaner although both bear the costs of the client frequently leaving in response to cheating (Bshary and Schäffer 2002). Cheating has been shown to correlate with the frequency of client jolts in response to cleaner fish mouth contact (Bshary and Grutter 2002; Soares, Bshary, Cardoso, and Côté 2008b). Bshary et al. (2008) observed that clients jolted less frequently during pair inspections than predicted from the sum of jolts caused by solitary male and female cleaner wrasses. In addition, in a controlled laboratory experiment, cleaners ate more of their less preferred food type when in pairs than as singletons (Bshary et al. 2008), which would translate into more cooperative behavior under natural conditions. Both results are in line with the cooperative solution predicted by the game theoretic model.

Here, we provide a new test of the model using cleaning gobies (*Elacatinus* spp), which are the most ubiquitous cleaners in the Caribbean region. The earlier study on cheating in paired *Labroides dimidiatus* used 2 indirect measures of dishonesty, namely, client jolts as a correlate of biting that is unrelated to the removal of ectoparasites and eating preferred prawn instead of less preferred fish flakes in a laboratory

experiment (see Bshary et al. 2008). Here, we used the most direct evidence of cheating: the ratio of scales to ectoparasites in stomach contents. Following the game theoretic model of Bshary et al. (2008), we predicted that this ratio should be lower in paired individuals than in singletons if cleaning goby pairs find a cooperative solution to the dilemma of cleaning with a partner. The model did not make specific predictions about the relative contribution of partners to increased service quality; however, Bshary et al. (2008) found that females behaved more cooperatively than males when paired. We therefore also investigated whether the same gender difference occurred in cleaning gobies.

MATERIALS AND METHODS

Study sites and species

The study was carried out on 8 fringing reefs on the west coast of Barbados, West Indies, between May and November 2005. All reefs were relatively degraded, with high macroalgal cover (~40%) and low live coral cover (~10%). Maximum depth ranged from 3 to 8 m, and all reefs exhibited a typical spur-and-groove formation at their seaward edge where fish collections were made. We focused on 2 closely related cleaning goby species *Elacatinus evelynae* (sharknose goby) and *Elacatinus prochilos* (broadstripe goby). These cleaning gobies are small (1.2–3.5 cm total length), and both species show a prominent lateral stripe (yellow or white) extending from the snout to the tail. They can be found on the surface of living coral (*Siderastrea* spp. and *Montastrea* spp.) or sponges. Sponge-dwelling cleaning gobies (mainly *E. prochilos*) feed primarily on nonclient-gleaned material (Arnal and Côté 2000; Whiteman and Côté 2002a). We therefore considered only cleaning gobies living on live coral. The 2 species, when living on live coral at the study location, do not differ in distribution (i.e., coral species and depth), client assemblages, or in their mean ratio of scales to ectoparasites ingested (Soares, Bshary, Cardoso, and Côté 2008a) and were therefore combined for analysis. The behavior of cleaning gobies has been described in detail elsewhere (Arnal and Côté 1998, 2000; Arnal et al. 2000, 2001; Cheney and Côté 2001, 2003, 2005; Whiteman and Côté 2002a, 2002b, 2003, 2004; Soares et al. 2007; Soares, Bshary, Cardoso, and Côté 2008a, 2008b; Soares, Côté, Cardoso, and Bshary 2008).

Behavioral observations

On each of the 8 study reefs, 20–22 cleaning stations were selected randomly. Each cleaning station was observed by a scuba diver only once, for 30 min, between 10 and 17 h, encompassing the hours of peak activity of both cleaning goby species (Johnson and Ruben 1988; Arnal and Côté 1998). These cleaning stations were operated either by a solitary adult cleaning goby (48 *E. evelynae* and 53 *E. prochilos* in total) or by a male–female breeding pair (31 *E. evelynae* pairs and 33 *E. prochilos* pairs in total). During each observation period, we recorded on plastic slates the species and size (total length estimated visually to the nearest centimeters) of each visiting client. Because cleaning gobies are site faithful and the location of observed cleaning stations was mapped, the likelihood of repeated observations of individual gobies was extremely low.

Gut content analysis

We collected 165 cleaning gobies across the 8 reefs, which had each been observed prior to capture to ascertain their paired status. To capture cleaning gobies, a mixture of clove oil (a natural anesthetic), ethanol, and water was sprayed over each individual fish, inducing a temporary reduction in activity. Gobies were then rapidly caught with hand nets and placed individually in sealed plastic bags filled with an overdose of clove oil to kill them. While still underwater, fish were transferred to 30-ml bottles filled with 75% alcohol to arrest digestion of gut contents. Once in the laboratory, each goby was measured to the nearest millimeter and sexed based on the shape of the urogenital papilla (long and conical in males and short, truncated, and often lobed in females; Whiteman and Côté 2002a, 2002b). Our sample included 77 *E. evelynae* (34 males and 43 females) and 88 *E. prochilos* (46 males and 42 females). Of these, 95 were paired (37 *E. evelynae* and 41 *E. prochilos*).

The entire gut (stomach and intestine) of each fish was dissected under a binocular microscope. The number of items in each of 4 main food categories (crustacean parasites, monogeneans, fish scales, and nonparasitic crustaceans) was counted. Mucus was found in only 5 of the gobies sampled and hence was not considered in this study. Ectoparasites were identified to family, focusing on the families Bomolochidae, Caligidae, Ergasilidae, Gnathiidae, Hatschekiidae, Kroyeriidae Myticolidae, Pandaridae, and also *Argulus* spp. Sample bottles were labeled with codes that did not allow the identification of paired status during gut content analysis, thus preventing inadvertent bias.

Ethical note

Examination of gut contents was necessary to obtain the most direct measure possible of dishonest cleaning in gobies. This measure could unfortunately only be obtained through destructive sampling. Nevertheless, we attempted to minimize stress and suffering of individual fish, as well as impacts on populations throughout the study. We minimized individual stress by proceeding as rapidly and efficiently as possible from capture to euthanasia (average time: ~3 min). We used clove oil as anesthetic because it has been shown to be highly effective (Woody et al. 2002) but causes little damage to the surrounding environment. Cleaning gobies exposed to a high dose of clove oil died quickly (<30 s) without exhibiting obvious signs of pain or distress. The 2 cleaning goby species studied are abundant on the study reefs and are not threatened. Although our sample size appears large, it comprises collections of no more than 22 cleaning gobies from each of 8 different reefs. These reefs were large (ranging in area from 30 000 to 60 000 m^2), and given the average densities of cleaning gobies present, our collections represent less than 1% of adults on the reefs. An experimental study of cleaning goby habitat preference showed that, after removal of resident gobies from patches on 2 of the study reefs used here, vacated areas were quickly recolonized by both adult and juvenile cleaning gobies, with the first new residents appearing within 2 weeks of removal (Whiteman and Côté 2004). Moreover, in a different study, the majority of experimentally divorced pairs of cleaning gobies on the same 2 reefs found a new mate in 7–9 days (Whiteman and Côté 2003). It therefore seems unlikely that our collections had a detrimental population-level impact.

Statistical analysis

Differences in clientele composition could influence cleaning goby dishonesty. We therefore carried out comparisons of client species composition between singletons and pairs of cleaning gobies using the software Plymouth Routines in Multivariate Ecological Research (PRIMER version 5.2.4; PRIMER-E Ltd, Plymouth Marine Laboratory, Plymouth, UK). An analysis of similarity (ANOSIM) was carried out on

the total number of visits by each client species recorded during each 30-min observation period. Each cleaning station ($N = 165$ stations in total) was considered a sample, and Bray–Curtis similarity coefficients between pairs of samples were computed (Clarke and Warwick 1994). Cleaning stations were grouped into 2 categories depending on the number of attending cleaning gobies. ANOSIM generates an R statistic, which ranges from 0 (i.e., as much similarity within as between categories) to 1 (i.e., all samples within a category are more similar to each other than to samples across categories) and which was tested for difference from zero with a permutation test ($N_{max} = 999$ permutations).

The propensity to cheat of each cleaning goby was measured by the ratio of the number of fish scales to the total number of ectoparasites it had ingested. These 2 item types were the most abundant in cleaning goby gut contents and were of similar sizes (~1 mm in length; Soares MC, personal observations). Cleaning gobies that had ingested no ectoparasites ($N = 4$) were removed from the analysis because we could not calculate a propensity to cheat for those fish. The cheating ratio was square-root transformed to achieve normality.

We examined the effect of cleaning goby pairing status (single vs. paired) and gender (and the interactions between these 2 variables) on the propensity of cleaning gobies to cheat by using a 3-way, mixed-model analysis of variance (ANOVA), with gender and pairing status (solitary–paired) as fixed factors and reef as a random factor. We also included cleaning goby total length as a covariate. Paired and solitary individuals did not differ in length or weight (between paired and single males: independent samples T test, total length: $t_{74} = -1.31$, $P = 0.19$; total weight: $t_{74} = -1.44$, $P = 0.15$; between paired and single females—total length: $t_{82} = 0.25$, $P = 0.80$; total weight: $t_{82} = 0.50$, $P = 0.62$). All tests were 2 tailed.

RESULTS

Overall, 37 different fish species were recorded visiting cleaning stations across the 8 study reefs. There was no significant difference in client species composition between cleaning stations operated by solitary individuals or by pairs of cleaning gobies (ANOSIM, $R = 0.04$, $P = 0.17$). Four client species accounted for the majority of interactions with both solitary (82.1% of interactions) and paired (77.1%) cleaning gobies. These were, in order of importance, the damselfishes *Chromis multilineata* and *Microspathodon chrysurus*, the goatfish *Mulloidichthys martinicus*, and the parrotfish *Scarus taeniopterus*.

Of the 161 gobies that had ectoparasites in their stomachs, 72.7% had also taken fish scales (mean ± 1 standard deviation = 24.2 ± 3.5 scales per goby, range = 0–310 scales goby per goby). Seventy-five percent of males and 73% of females had eaten fish scales.

Overall, the cheating index did not differ significantly between solitary and paired individuals (3-way ANOVA, $F_{1,129} = 0.66$, $P = 0.44$). The cheating index was also similar between male and female cleaning gobies ($F_{1,129} = 1.39$, $P = 0.28$). However, the interaction between pairing status and gender was significant ($F_{1,129} = 8.56$, $P = 0.02$). Post hoc analyses revealed that males showed a nonsignificant tendency to become more cooperative when living in pairs ($T_{74} = 1.77$, $P = 0.08$; Figure 1), whereas females did not alter their behavior significantly ($T_{82} = -1.19$, $P = 0.24$; Figure 1). In addition, solitary males had ingested a significantly higher ratio of scales to ectoparasites than solitary female gobies ($T_{84} = 2.55$, $P = 0.01$; Figure 1), whereas this difference disappeared in paired individuals ($T_{73} = -0.64$, $P = 0.52$; Figure 1). The propensity to cheat of cleaning gobies did not vary across the study reefs (3-way ANOVA, $F_{7,129} = 2.38$, $P = 0.19$) or with cleaning goby total length ($F_{1,128} = 2.43$, $P = 0.12$).

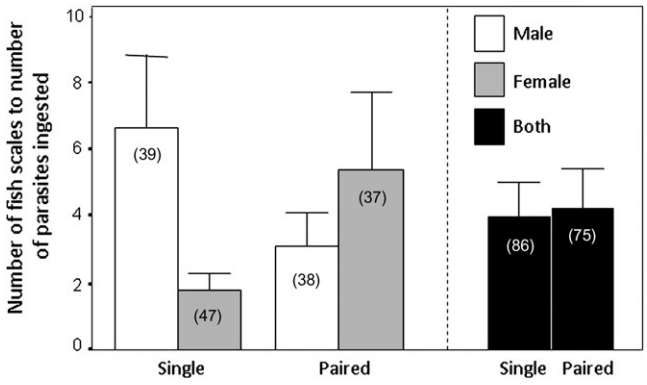

Figure 1
The propensity to cheat, measured as the number of ingested scales to ectoparasites, by cleaning gobies cleaning solitarily or in male–female pairs. Means are shown ± 1 standard error for each gender separately (white and gray bars) and for the genders combined (black bars). Sample sizes (=number of cleaning gobies) are given in parentheses.

DISCUSSION

Caribbean cleaning gobies deal with the dilemma of cleaning with a partner in a fundamentally similar way as the cleaner wrasse *L. dimidiatus*: in both species, cleaning in pairs does not lead to an escalation in cheating and hence to the breakdown of cleaning mutualism. However, our results do not fully support the cooperative solution predicted by the game theoretic model of Bshary et al. (2008) but rather seem to fit the null hypothesis that service quality would tend to be similar during singleton and pair inspections. The results pooled across genders as well as those for females agree with the null hypothesis, whereas only males tended to corroborate, although marginally nonsignificantly so, the cooperative prediction of the model. Thus, the gender-specific strategies of cleaning gobies differ from those of *L. dimidiatus*, where both sexes behaved more cooperatively during the pair situation and females significantly more so than males (Bshary et al. 2008).

The observed differences between Caribbean cleaning gobies and Indo-Pacific cleaner wrasses in their responses to cleaning in pairs could stem from key differences in cleaner–client interactions. The most important may be that the clients of cleaner wrasses cause cleaners to reduce cheating in various ways: predatory clients through the threat of reciprocating cheating by trying to eat the cleaner, nonresident clients by switching to another cleaner in response to cheating, and resident clients by punishing the cleaner after poor cleaning service, which improves future service quality (Bshary 2001; Bshary and Schäffer 2002; Bshary and Grutter 2005). In contrast, clients of cleaning gobies simply leave in response to cheating without chasing the cleaner or withholding return to that cleaning station (Soares, Côté, Cardoso, and Bshary 2008). These differences in client behaviors may in turn be explained if cleaning gobies, in contrast to *L. dimidiatus* (Grutter and Bshary 2003), prefer ectoparasites over client mucus. Such a preference would lead cleaning gobies to invariably begin interactions with clients cooperatively and perhaps switch to mucus and scale feeding only once ectoparasites are depleted (Soares, Côté, Cardoso, and Bshary 2008). Their preferences should therefore not be influenced by the presence of a second cleaning goby. As long as jolts cause clients to leave with a fixed probability, independently of the number of cleaners, overall service quality would remain similar whether gobies inspect alone or in pairs.

Alternative explanations for the overall lack of difference in service quality between solitary and paired cleaning gobies include cognitive constraints, inherent differences associated with pairing status, and confounding factors. We consider it unlikely that cognitive constraints prevent cleaning gobies from finding the solution that was predicted by the game theoretic model (Bshary et al. 2008). Whereas it is clear that cleaner wrasses show a more flexible service quality that varies with client species identity and manipulate client decisions (Bshary and Côté 2008), the service quality of male cleaning gobies appeared to be variable in the present study (see below). We did not have matched data for the same individuals in solitary and paired situations. We can therefore not exclude the possibility of differences—other than length and weight, which we did examine—between solitary and paired individuals that affect propensity to cheat, although such differences would affect males only. Finally, it should be noted that paired cleaning gobies sometimes clean alone, for example, when 2 clients arrive simultaneously at a station (Whiteman and Côté 2002a, 2002b). Therefore, the stomach content analyses of paired individuals presented here may partly reflect solitary cleaning and hence mask differences between paired and solitary cleaning gobies.

A key difference between cleaning gobies and cleaner wrasses was the opposite responses of the sexes to joint cleaning: in cleaning gobies, the males tended to become more cooperative (this study), whereas in cleaner wrasses, females did so more than males, largely because male cleaner wrasses seem to coerce their female partners into cooperative behavior through aggression (Bshary et al. 2008). The differences between cleaning gobies and cleaner wrasses may be explained by differences in their social and mating systems. Cleaner wrasses are protogynous hermaphrodites; individuals first breed as females and eventually change sex to become male harem owners (Robertson 1972, 1974). In such mating systems, females enhance their growth with a decrease in fecundity (Sakay 1997), creating a conflict between the reproductive interests of males, who gain from sexual monopoly over highly fecund females, and those of females, who would benefit most by changing sex. Thus, any foraging benefit of cheating gained by female wrasses is a potential threat to male control, explaining male cleaner wrasse coercion of females into honest cleaning when cleaning together. Cleaning gobies, in contrast, do not change sex and have strictly monogamous, long-term relationships with multiple spawning cycles (Harding et al. 2003; Whiteman and Côté 2003). In such a mating system, the reproductive success of males and females are highly interdependent (Roberts 2005), and male cleaning gobies may become more cooperative when cleaning in pairs as a form an investment into their partner's fecundity.

In conclusion, our study suggests that the game theoretic model of pairs of service providers holds on a very general level for cleaning mutualisms because an escalation of cheating does not occur when cleaners clean in pairs. However, the specific features of interactions between clients and cleaners, which vary in different cleaner species, appear to influence the outcome of pair cleaning. Furthermore, our study highlights the need to explore in more detail how variation in social systems may affect sex-specific behavioral strategies during pair inspections and hence overall service quality.

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